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ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Tree species effects on ecosystem water-use efficiency in a high-elevation, subalpine forest

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Abstract Ecosystem water-use efficiency (eWUE; the ratio of net ecosystem productivity to evapotranspiration rate) is a complex landscape-scale parameter controlled by both physical and biological processes occurring in soil and plants. Leaf WUE (lWUE; the ratio of leaf CO_2 assimilation rate to transpiration rate) is controlled at short time scales principally by leaf stomatal dynamics and this control varies among plant species. Little is known about how leaf-scale variation in lWUE influences landscape-scale variation in eWUE. We analyzed approximately seven thousand 30-min averaged eddy covariance observations distributed across 9 years in order to assess eWUE in two neighboring forest communities. Mean eWUE was 19% lower for the community in which Engelmann spruce and subalpine fir were dominant, compared to the community in which lodgepole pine was dominant. Of that 19% difference, 8% was attributed to residual bias in the analysis that favored periods with slightly drier winds for the spruce-fir community. In an effort to explain the remaining 11% difference, we assessed patterns in lWUE using C isotope ratios. When we focused on bulk tissue from older needles we detected significant differences in lWUE among tree species and between upper and lower canopy needles. However, when these differences were scaled to reflect vertical and horizontal leaf area distributions within the two communities, they provided no power to explain differences in eWUE that we observed in the eddy covariance data. When we focused only on bulk needle tissue of current-year needles for 3 of the 9 years, we also observed differences in lWUE among species and in needles from upper and lower parts of the canopy. When these differences in lWUE were scaled to reflect leaf area distributions within the two communities, we were able to explain 6.3% of the differences in eWUE in 1 year (2006), but there was no power to explain differences in the other 2 years (2003 and 2007). When we examined sugars extracted from needles at 3 different times during the growing season of 2007, we could explain 3.8–6.0% of the differences in eWUE between the two communities, but the difference in eWUE obtained from the eddy covariance record, and averaged over the growing season for this single year, was 32%. Thus, overall, after accounting for species effects on lWUE, we could explain little of the difference in eWUE between the two forest communities observed in the eddy covariance record. It is likely that water and C fluxes from soil, understory plants, and non-needle tissues, account for most of the differences observed in the eddy covariance data. For those cases where we could explain some of the difference in eWUE on the basis of species effects, we partitioned the scaled patterns in lWUE into two components: a component that is independent of canopy leaf area distribution, and therefore only

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dependent on species-specific differences in needle physiology; and a component that is independent of species differences in needle physiology, and only dependent on species-specific influences on canopy leaf area distribution. Only the component that is dependent on species influences on canopy leaf area distribution, and independent of inherent species differences in needle physiology, had potential to explain differences in eWUE between the two communities. Thus, when tree species effects are important, canopy structure, rather than species-specific needle physiology, has more potential to explain patterns in eWUE.

Keywords Hydrology · Coupled biogeochemical cycles · Conifers · Mountain · Biodiversity

Introduction

Ecosystem water-use efficiency (eWUE), the ratio of net ecosystem productivity to evapotranspiration rate (NEP/ET), is a broadly used synthetic ratio capable of informing us as to the effective coupling between the water and C cycles. The ratio has been used as a parameter in ecosystem process models (Law et al. 2000; Del Grosso et al. 2008; Jansson et al. 2008) and in evaluating ecosystem management options in the face of future climate change (Emmerich 2007; Yu et al. 2008). The concept of WUE originally arose from leaf- and plant-scale studies of stomatal control over CO_2 and H_2O fluxes, and theory that was originally developed at the leaf scale forms the foundation of most ecosystem- and global-scale models of eWUE (e.g., Sellers et al. 1996; Bonan 1996; Pyles et al. 2000). As efforts progress to develop the concept of eWUE in ecosystem modeling and management it will be valuable to continue testing the potential for leaf-scale WUE (lWUE) to successfully inform projections of eWUE.

There is no a priori reason for optimism in merging the concept of WUE at these scales. At the ecosystem scale, eWUE is influenced by both plant and soil processes; soil fluxes can be large (Bolstad et al. 2004; Lee et al. 2006; Sacks et al. 2006) and potentially swamp the signals from leaf fluxes (Goulden et al. 1998). Additionally, CO_2 and H_2O fluxes can be influenced by scale-dependent processes that produce emergent properties, uniquely affecting observations at the highest scales (e.g., Gu et al. 1999; Knohl and Baldocchi 2008). Two of the most important emergent properties that influence how lWUE may affect eWUE are canopy structure (which can alter the microenvironment of individual leaves) and community species composition (which can alter the proportional abundance of leaves from species with different evolutionary histories). Sun leaves have higher photosynthetic rates and tend to operate at higher lWUE, compared to shade leaves (Carter and Smith 1985; Francey et al. 1985; Berry et al. 1997; Le Roux et al. 2001; Niinemets et al. 2004; Duursma and Marshall 2006). Shifts in the relative abundance of sun and shade leaves may have important consequences for eWUE, and species are known to differ in their plant crown architecture and placement of leaves within the canopy (Cescatti and Niinemets 2004). There is also genetically controlled variation among species in stomatal densities and guard cell properties (Domingues et al. 2006; Golluscio and Oesterheld 2007), and this variation is highly dependent on the canopy environment in which leaves develop (Gonzalez-Rodriguez et al. 2002; Peters et al. 2008). Thus, the collections of species that make up a community, variation in canopy microclimate, and unique stomatal properties among species have the potential to exert significant control over eWUE.

We made observations of forest-atmosphere CO_2 and H_2O exchanges using a tower-based eddy covariance system for 9 years above a subalpine forest ecosystem. The tower is located in the ecotone between two forest communities—one dominated by lodgepole pine and one dominated by Engelmann spruce and subalpine fir. In analyzing our flux record we were able to distinguish differences in eWUE depending on wind direction and whether fluxes were recorded from one community or the other. In this study we addressed the question: can we explain the observed differences in eWUE between these two communities through analysis of lWUE?

Materials and methods

Field site

The study was conducted at the Niwot Ridge AmeriFlux tower site (40°1′58.4″N, 105°32′47.0″W), at 3,050 m elevation, located in Colorado, USA. The forest is approximately 100 years old having regenerated naturally following heavy logging. The dominant tree species in the forest are *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Pinus contorta* (lodgepole pine). The understory is relatively sparse, containing seedlings from all three tree species and patches of *Vaccinium myrtillus* (25% average understory coverage). Mean annual precipitation averages 800 mm (approximately 65% falling as snow) and the mean annual temperature is 1.5°C.

Eddy covariance measurements

The eddy covariance method was used to measure CO_2 and H_2O fluxes as described in past papers (Monson et al. 2002; Turnipseed et al. 2003). Comprehensive analyses of advective fluxes at the site, and their influence on estimates of cumulative C uptake rates have been reported in Yi et al. (2008). In general, while advective fluxes can cause errors in estimates of the local C budget, this is only significant when considering nighttime fluxes; in this paper we consider only daytime fluxes. The storage of CO_2 within the canopy was measured using a profile system (Monson et al. 2002). The change in stored CO_2 was added to the calculated eddy flux to provide net ecosystem CO_2 productivity (NEP). By convention, NEP is considered positive in sign when the net CO_2 flux is from the atmosphere to the forest and negative when the net flux is from the forest to the atmosphere.

Ecosystem WUE was calculated from non gap-filled 30-min averaged fluxes. In order to characterize fluxes differentially for the two forest communities, we assembled observation "bins" when the wind direction was from the east (80–100°, with 0° indicating north) or west (260°–280°). Observations were included for comparison only when 30-min periods with averaged easterly or westerly winds (recorded at 21.5 m height) occurred in the same day, and when mean values for certain environmental parameters were similar among those periods: atmospheric vapor pressure deficit (VPD) within 0.5 kPa, air temperature within 5°C, wind speed within 2 m s^{-1}, surface friction velocity ($u*$) at 21.5 m within 0.3 m s^{-1}, and photosynthetic photon flux density (PPFD) within 200 μmol m^{-2} s^{-1}. Additionally, we only used data when the $u*$ value was greater than 0.2 m s^{-1}, thus avoiding relatively stable atmospheric conditions, and when PPFD was greater than 700 μmol m^{-2} s^{-1}, which has been shown to saturate observed NEP in our previous studies (Monson et al. 2002). Thus, our analysis is only relevant to midday periods when we expect tree CO_2 assimilation rates to be highest.

Climate data for the study period were obtained from the data archives of the Niwot Ridge AmeriFlux site (http://urquell.colorado.edu/data_ameriflux/). Precipitation was measured using a heated tipping bucket rain/snow gauge (Met One, Grants Pass, Ore.) with a datalogger. Soil moisture was measured at two depths (5 and 15 cm) using time-domain reflectometry probes (models CS615 and CS616; Campbell Scientific, Logan, Utah). It should be noted that soil moisture was only measured in a single plot near the AmeriFlux tower, and therefore our data do not provide a measure of differential soil moisture in the two forest communities.

Forest community characterization

We measured leaf area index (LAI) and species composition for the two forest communities using two different campaigns (in 1999 and 2006). Here, LAI is defined as leaf (needle) area per unit ground area. We destructively harvested trees of different sizes for each of the three dominant species ($n = 5$ for each species in 1999 and $n = 4$ in 2006) to determine allometric scaling relations. In both campaigns, tree canopies were divided into sections, with branches and needles subsampled from each section to determine needle biomass. Needle area was calculated from linear regressions between needle dry mass and area; with total needle area determined using the volume displacement method and knowledge of needle cross-section geometry (Chen et al. 1997). Total needle area was converted to projected (hemispheric) needle area (HSA) using an angular light table (Fassnacht et al. 1994).

Tree HSA was scaled to the landscape using two different approaches. In 1999, the diameter at breast height (DBH) was determined for all trees within a 100-m × 100-m area to the east and west of the tower, and for all trees within 14 (seven east and seven west) 400 × 1-m belt transects. The HSA of individual trees was estimated from the allometric relations obtained from the 1999 harvest, and converted to LAI by multiplying the area per tree by the number of trees of each respective DBH size class in each of the sampled plots and transects and dividing by the area of the plot or transect. In 2006, we used mapped plots east and west of the tower to provide tree distribution for all trees over 1 m in height. Eighteen 10-m × 10-m plots located along a transect extending 180 m east and west from the flux tower location were mapped (632 trees) using a hand-held Geographic Positioning System (GPS; Trimble 5800 GPS survey system; Trimble, Sunnyvale, Calif.). We also recorded DBH, crown and tree height (using triangulation), and base of crown diameter in the north–south and east–west axes (using a calibrated pole). Hemispheric needle area and its vertical distribution were determined for these trees using the allometric equations developed from the 2006 harvests. These data were used to construct maps of the vertical and horizontal leaf area distribution using ESRI ArcScene software (ESRI, Redlands, Calif.). Maps were created by assigning a leaf area for each pixel of each plot (ArcGIS 9.2; ESRI) and buffer layers of leaf area per pixel were created for each 1-m vertical canopy section. Rasters were created for each buffer layer of needle area and these rasters were then summed across layers.

Needle tissue and needle sugar C isotope ratios

In order to assess lWUE we conducted these separate analyses:

1. Tissue $^{13}C/^{12}C$ ratios (stable C isotope ratio; $\delta^{13}C$) were measured for needles produced at least 1 year prior to collection. These needles were collected and analyzed separately at two heights (upper half of the crown and lower half of the crown, designated as

"sun" and "shade" needles, respectively) for all three species east and west of the flux tower, during midsummer (5 June–15 July) 2003. Sun needles were only taken from that part of the tree crown where the canopy had consistent unobstructed exposure to the sky. Shade needles were taken from at least 0.1 m inside the tree crown envelope in the lower part of the canopy, where shaded conditions occurred for most of the day. We systematically collected branches from each of the four cardinal directions of the crown of each tree and each height. After ANOVA analysis showed that crown direction had no significant effect on δ^{13}C value, we pooled the data for all four directions at each height and for each tree. In making this collection, we pooled approximately equal amounts of needles from all portions of the stem, beginning with those located below the current year needles. The needles of all three species have relatively high longevities (5–22 years for lodgepole pine, 9–18 years for Engelmann spruce, and 8–15 years for subalpine fir; Schoettle and Fahey 1994; Anna Schoettle, USDA Forest Service, personal communication); meaning that the results of this analysis likely reflected the lWUEs of numerous seasons across numerous years.

2. Tissue δ^{13}C were measured for sun needles collected in October of the same year they were produced, in 3 different years (2003, 2006, 2007), for all three species. In making this collection we aimed to examine interannual and single-year differences in lWUE.
3. δ^{13}C were measured for needle sugars extracted from sun and shade needles collected 3 times during the growing season of 2007 (6 June, 6 July, 14 August). In conducting these measurements, we aimed to examine within-season differences in lWUE.

Needle and sugar δ^{13}C ratios were determined by mass spectrometry at the University of Wyoming Stable Isotope Facility or at the University of California (Berkeley) Center for Stable Isotope Biogeochemistry. We developed procedures for isolating the recently synthesized sugars in needle tissues following the protocol of Gessler et al. (2001). After collection, needles were immediately frozen in liquid nitrogen. In the lab, the needles were freeze-dried and ground to a fine powder. Soluble sugars were extracted from 150 mg of ground needle tissue at 10°C for 1 h using 150 mg of polyvinylpyrrolidone and 2 ml of distilled water, followed by boiling for 2 min. The samples were centrifuged at 12,000 g for 10 min, and the supernatant was decanted and frozen at −20°C. Needle extract (450 µl) was pipetted into a sample tin, dried in the oven for 48 h at 60°C and then analyzed for δ^{13}C.

We used the δ^{13}C of needles and needle sugars, as a means to estimate the intercellular CO$_2$ concentration (c_i), which when combined with knowledge of the atmospheric CO$_2$ concentration (c_a) and the leaf-to-air water vapor pressure difference (v) can be used to estimate lWUE:

$$\mathrm{lWUE} = \mathrm{A/T} = (c_a - c_i)/1.6v \tag{1}$$

where 1.6 is the ratio of the diffusivity of water vapor in air to the diffusivity of CO$_2$ in air. v is calculated as:

$$v = [e_s - e_a] \tag{2}$$

where e_s is saturated vapor pressure and e_a is actual vapor pressure of the ambient air. Inherent in this relationship is the assumption that needle temperature equaled air temperature. We used 30-min averaged values for air temperature and relative humidity collected from the flux tower at 21.5 or 2 m, for calculating v for upper and lower canopy needles, respectively; thus accounting for vertical differences in temperature and humidity within the canopy. We have made independent measurements of needle and air temperature on many occasions in our past research on all three species and have found that the two are closely coupled and nearly equal throughout the day; the site is typically windy during daytime periods, and the needles are narrow, which facilitates good convective coupling between needle and air temperature. Equations 1 and 2 were solved for mean values between the hours of 9 a.m. and 3 p.m. for: (1) the period between 1 May and July 2003 for analysis of the >1 year old needles, (2) between 1 May and 1 October in each respective year of collection for analysis of the current-year needles, and (3) for the 2-week period prior to sample collection for analysis of the needle sugars. In order to estimate c_i in Eq. 1 we followed the theory presented in Farquhar et al. (1989):

$$\Delta = a + (b - a)c_i/c_a \tag{3}$$

where a is the fractionation of ^{13}C and ^{12}C during diffusion through the stomata (assumed as 4.4‰), b is the biochemical fractionation during carboxylation (assumed as 27‰), and Δ is the isotope discrimination factor and is defined as:

$$\Delta = \left(\delta^{13}\mathrm{C_a} - \delta^{13}\mathrm{C_s}\right)/\left(1 + \delta^{13}\mathrm{C_s}\right) \tag{4}$$

where $\delta^{13}\mathrm{C_a}$ reflects the isotopic ratio of the atmosphere and $\delta^{13}\mathrm{C_s}$ reflects the isotopic ratio of the sample (needle tissue or sugars). We used atmospheric $\delta^{13}\mathrm{C_a}$ values of −8.5 and −9.0‰, and c_a of 380 and 390 p.p.m., for the calculation of lWUE of upper and lower canopy needles, respectively. These values represent the approximate means obtained from flux tower observations using a tunable diode laser (see Schaeffer et al. 2008).

Our analysis relies on the linear model (Eq. 3) of isotopic fractionation and ignores influences of internal CO$_2$ transfer and photorespiration, both of which are known to influence Δ (Farquhar et al. 1989). By ignoring these influences it is possible to overestimate the WUE estimated from tissue δ^{13}C values (Seibt et al. 2008). We conducted an analysis to evaluate the magnitude of this overestimation in our own studies. We used the linear and classic forms of the model for Δ as defined in Seibt et al. (2008), and we used the following additional assumptions to parameterize the classic form of the model: the photocompensation point = 30 p.p.m., and mesophyll fractionation = 1.8‰. The results of this comparative analysis are presented in the "Discussion".

We used the various sets of δ^{13}C data described above to estimate lWUE for plots of known species composition and LAI distribution east and west of the tower. We used the same 18 plots (nine west and nine east of the tower) that were used for allometric analysis in 2006. We separately partitioned the effects of differential species physiology and canopy structure for each of the three C isotope analyses described above. The species physiology effect was calculated using the combined mean of upper and lower canopy needles (thus averaging out the canopy structure effects) lWUE (f, s, or p for fir, spruce or pine, respectively) and multiplied by the fraction of LAI (*L*) of that species for each plot.

$$\mathrm{lWUE} = \mathrm{lWUE_f}\,\mathrm{L_f} + \mathrm{lWUE_s}\,\mathrm{L_s} + \mathrm{lWUE_p}\,\mathrm{L_p}. \qquad (5)$$

The effect of differential canopy structure was estimated using species-averaged values for sun and shade needles, and multiplied by the fractional *L* for sun (su) or shade (sh) needles:

$$\mathrm{lWUE} = \mathrm{lWUE_{sh}}\,\mathrm{L_{sh}} + \mathrm{lWUE_{su}}\,\mathrm{L_{su}} \qquad (6)$$

The combined effect of both species physiology and canopy structure was calculated as:

$$\begin{aligned}\mathrm{lWUE} = {}& \mathrm{lWUE_{f,su}}\,\mathrm{L_{f,su}} + \mathrm{lWUE_{f,sh}}\,\mathrm{L_{f,sh}} + \mathrm{lWUE_{s,su}}\,\mathrm{L_{s,su}} \\ & + \mathrm{lWUE_{s,sh}}\,\mathrm{L_{s,sh}} + \mathrm{lWUE_{p,su}}\,\mathrm{L_{p,su}} + \mathrm{lWUE_{p,sh}}\,\mathrm{L_{p,sh}}.\end{aligned} \qquad (7)$$

Statistical analyses

Leaf area data and C isotope data were analyzed using an ANOVA (PROC MIXED; SAS, version 9.1; SAS Institute, Cary, N.C.). All regressions were tested using PROC REG. Post hoc analyses were performed using Tukey's corrections for multiple comparisons and considered significant when $P \leq 0.05$. Plots within the site were considered replicates and therefore inferences were limited to this site only. We assessed the significance of differences in NEP, ET and eWUE between the eastern and western forest communities when paired for each successive week of the growing season using an ANOVA. The random error of flux measurements was estimated using a daily differencing approach (Richardson et al. 2006); this analysis revealed that the error distribution was best described by a double-exponential probability distribution. Bootstrap pseudoreplicates were created using an original flux observation plus a random uncertainty term derived from the double-exponential distribution. These replicates were then used to estimate 95% confidence intervals around the mean flux.

Results

In order to characterize eWUE for the two forest communities and across the growing season, we binned 30-min flux periods within each day by wind direction and selecting periods with similar climate and wind regimes as described above. When considered over the 9-year flux record, this resulted in 6,948 total 30-min periods, with 45% of the periods reflecting easterly winds (across the pine-dominated forest) and 55% reflecting westerly winds (across the spruce-fir dominated forest). When partitioned according to month during the growing season, the periods were divided as 16, 22, 24, 25 and 13% for the months of May, June, July–August and September, respectively. With respect to year, the observation periods divided according to 6.1% (1999), 11.4% (2000), 11.8% (2001), 10.0% (2002), 11.5% (2003), 9.1% (2004), 14.6% (2005), 11.9% (2006), and 13.6% (2007). Thus, there was no extreme bias in the data used to evaluate eWUE, either with respect to wind direction, month or year. When all periods were considered, the pine-dominated forest exhibited higher rates of NEP and ET, and higher eWUE, compared to the spruce-fir dominated forest during most of the growing season (Fig. 1a–c). The exception to this pattern occurred during the middle of the summer (late June to mid-July, weeks 27–31) after the soil had dried considerably following the snow-melt period. When averaged across all growing season months (May–October), and for all 9 years, the pine-dominated community exhibited a WUE that was 19% higher than the spruce-fir community.

Seasonal and interannual differences in eWUE are shown in Fig. 2. Values of eWUE were highest and most often different between the two communities during June. In July and August, eWUE was not different between the communities, except for 1 year, 2007, in August. In examining the weekly means for NEP and ET, across all 9 years, we also found a slight bias toward lower NEP at a given ET (Fig. 3).

After binning all growing season fluxes, there remained some residual micrometeorological bias in the easterly versus westerly bins. Across all 9 years, the two bins had mean air temperatures that differed by 0.7°C, with westerly winds being warmer, and VPDs that differed by 0.2 kPa, with westerly winds being drier (Fig. 4). We plotted the

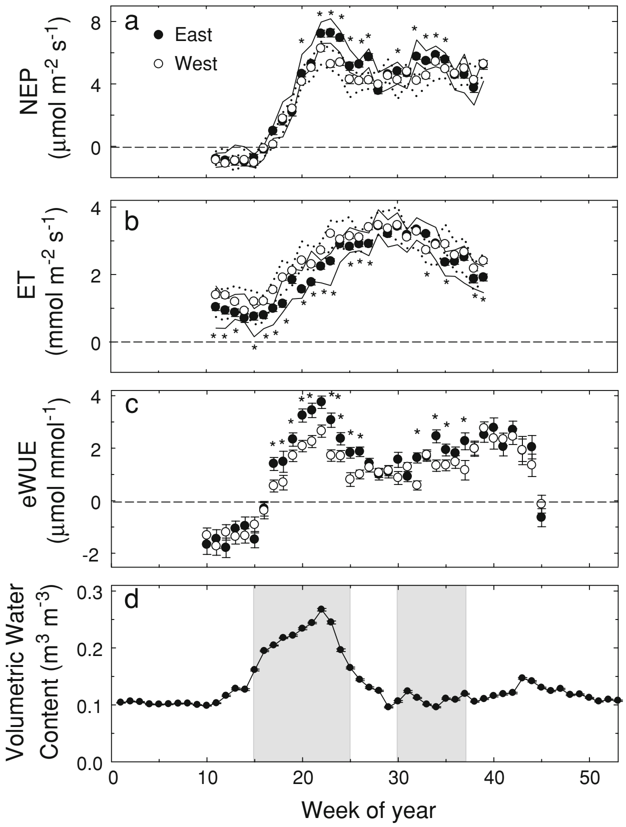

Fig. 1 Weekly mean net ecosystem production (*NEP*; **a**), evapotranspiration (*ET*; **b**), ecosystem water-use efficiency (*eWUE*; **c**), and volumetric soil water content (**d**). Least squares mean ± SE (*vertical bars*) were calculated using ANOVA. The *dotted* and *solid lines* bounding the trends show the 95% confidence intervals constructed using the bootstrapped random error approach (see "Materials and methods"). **d** *Gray shading* indicates times when significant differences occurred between east and west in the eWUE. **a–c** Measurements plotted from 30-min averaging periods with similar climatic conditions for each ecosystem for each week, after calculating weekly mean and SE. $^*P < 0.05$ (between east and west fluxes)

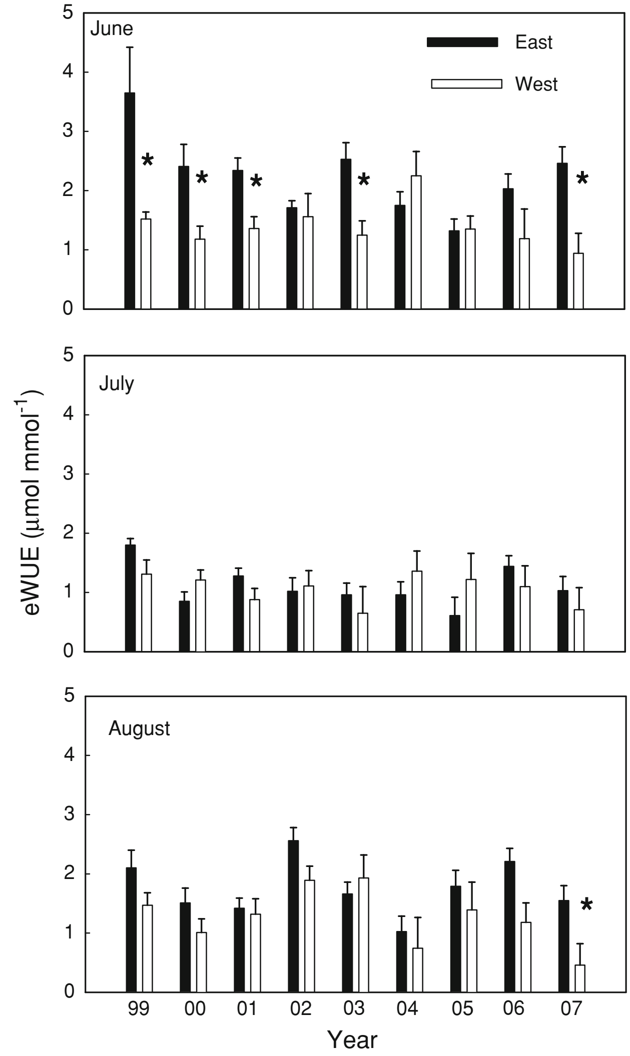

Fig. 2 Differences in eWUE among years and for the three midsummer months of June, July and August. *Vertical bars* are SE. $^*P < 0.05$ [between the east (pine-dominated) and west (spruce-fir dominated) communities]

responses of ET and NEP to these differences and estimated that the residual biases would cause an 8% higher ET and 0.03% higher NEP in periods with westerly winds.

The forest community east of the flux tower had a higher abundance of lodgepole pine and lower abundance of spruce and fir, relative to the forest community west of the tower (Table 1). Total aboveground biomass and total needle biomass were higher in the spruce-fir dominated community. When both LAI measurement campaigns (1999 and 2006) were combined, they provided a mean estimate of 3.8 m^2 m^{-2} for the overall Niwot Ridge forest, 3.5 m^2 m^{-2} for the pine-dominated community and 4.0 m^2 m^{-2} for the spruce-fir dominated community.

The three dominant tree species were easily distinguishable on the basis of crown shape and structure (Fig. 5). Fir trees were conical with long branches in the lower canopy. Spruce trees had wide, cylindrical crowns and pine trees had relatively compact crowns. The vertical distribution of hemispherical needle area differed among the species (Fig. 6). The needle area of pine trees occurred predominantly in the upper crown, except for the smallest trees (<10 cm DBH). Spruce trees carried most leaf area in the upper two-thirds of the crown. Fir trees had evenly distributed foliage at all heights. When scaled to the forest stand, the spruce-fir community had greater overall leaf area in both the upper and lower levels of the canopy, but the pine community carried 85% of its needle area in the upper two-thirds of the canopy compared to only 69% in the spruce-fir community (Fig. 7).

In order to assess differences in δ^{13}C of needles, and thus lWUE, we conducted three different sets of sample collections and analyses (Table 2; see "Materials and methods"). In general, calculated values for lWUE differed

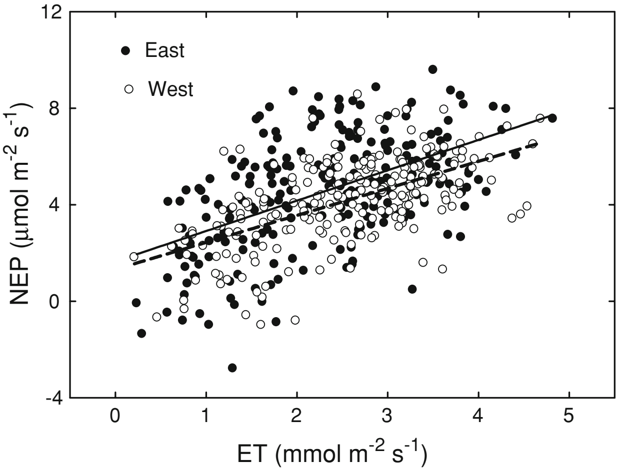

Fig. 3 The relationship between weekly mean NEP and weekly mean ET across all 9 years and pooled for the entire growing season in each year (May–October). Regression equations were $y = 1.259x + 1.65$ for the eastern (pine-dominated) community ($n = 228$, $r^2 = 0.28$, $P < 0.0001$) and $y = 1.1191x + 1.32$ for the western (spruce-fir dominated) community ($n = 228$, $r^2 = 0.33$, $P < 0.0001$). For abbreviations, see Fig. 1

with regard to species, canopy position and year, with some interactions terms between these variables being significant (Table 3). In general, fir needles had the lowest lWUE and spruce needles the highest. The one exception to this pattern occurred in the current needle collection of 2003, in which fir needles exhibited a high lWUE. This is likely due to the fact that the growing season of 2002, the year prior to the collection, was the driest season recorded in the past 100 years. Clearly, the needles of fir responded to this extremely dry year more than the needles of pine or spruce, by increasing their lWUE.

Using the relative distribution of trees in the two forest communities, lWUE was scaled to specific plots and averaged among plots (Table 4). We assumed that these scaled values of lWUE provided an opportunity to explain, or not explain, the contribution of species differences in lWUE to differences in eWUE that were observed in the eddy covariance data. We also used Eqs. 5, 6 and 7 to partition any differences in scaled lWUE between the two forest communities into those components due to species affinity alone, vertical distribution of LAI alone, or a combination of both. For the needles greater than 1 year in age, we found no potential for species affinity alone, or for species affinity combined with LAI distribution, to explain differences in scaled lWUE between the two forest communities. For LAI distribution alone, we could explain 2.7% of the difference in scaled lWUE between the two communities. When we focused on current-year needles, we found that the combination of species affinity and LAI distribution could only explain a significant amount of the difference in scaled lWUE in the two forest communities in 2006; there was no power to explain these differences in 2003 or 2007. When lWUE obtained from the sugar data (collected in 2007) was used in the analysis, significant differences were projected for the two communities, ranging from 3.8 to 6% for all three dates during the growing season.

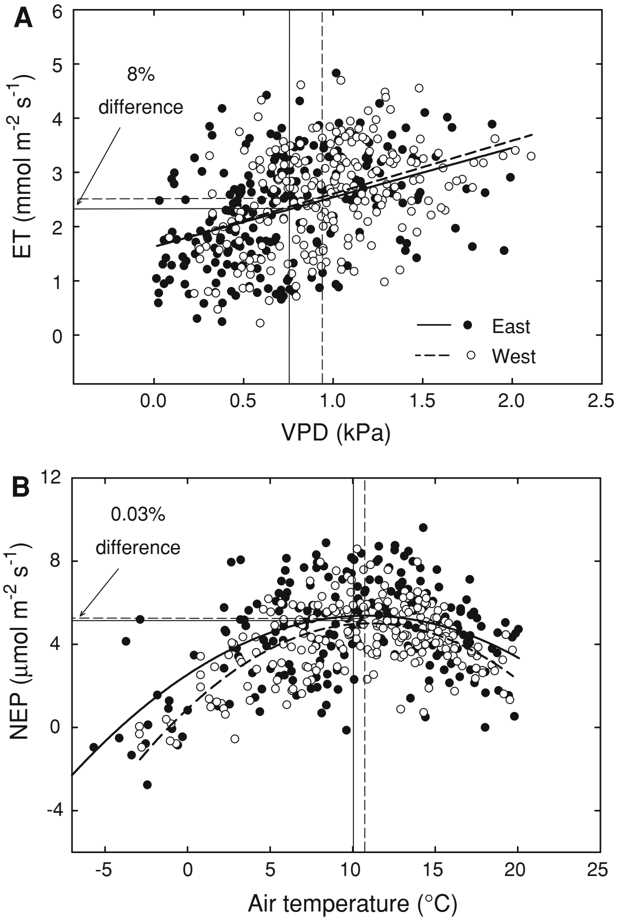

Fig. 4 **a** ET versus atmospheric VPD, and **b** NEP versus air temperature, for weekly averaged data. Each weekly average contains data only for those 30-min periods that were chosen for the analysis presented in Fig. 1. The mean VPDs and air temperatures for periods with easterly or westerly winds are shown as the *vertical solid lines* and *dashed lines*, respectively, and these residual differences extrapolate to the differences shown on the *y*-axis. For abbreviations, see Fig. 1

Discussion

Ecosystem C and water fluxes are controlled at a variety of scales by numerous underlying processes; some of the most important controls can be assigned to the inherent physiological and morphological traits of species (Hooper et al. 2005). In those circumstances where species traits exert measurable control over ecosystem processes, an

Table 1 Stand characteristics of the forest to the east and west of the Niwot Ridge AmeriFlux tower

	East	West
Tree distribution		
Abies lasiocarpa	0.10 ± 0.006 Trees m^{-2}	0.16 ± 0.01 Trees m^{-2}
Picea engelmannii	0.07 ± 0.003 Trees m^{-2}	0.10 ± 0.003 Trees m^{-2}
Pinus contorta	0.27 ± 0.008 Trees m^{-2}	0.09 ± 0.003 Trees m^{-2}
Total	0.44 ± 0.017 Trees m^{-2}	0.35 ± 0.016 Trees m^{-2}
Total aboveground biomass	22.41 kg m^{-2}	24.17 kg m^{-2}
Leaf biomass	3.54 kg m^{-2}	4.02 kg m^{-2}
LAI (1999)	3.8 ± 0.3 m^2 m^{-2}	4.2 ± 0.4 m^2 m^{-2}
LAI (2006)	3.1 ± 0.3 m^2 m^{-2}	3.8 ± 0.3 m^2 m^{-2}

Error estimates equal ± 1 SE. The two leaf area index (*LAI*) estimates refer to the two different campaigns used to construct biometric estimates of LAI distribution

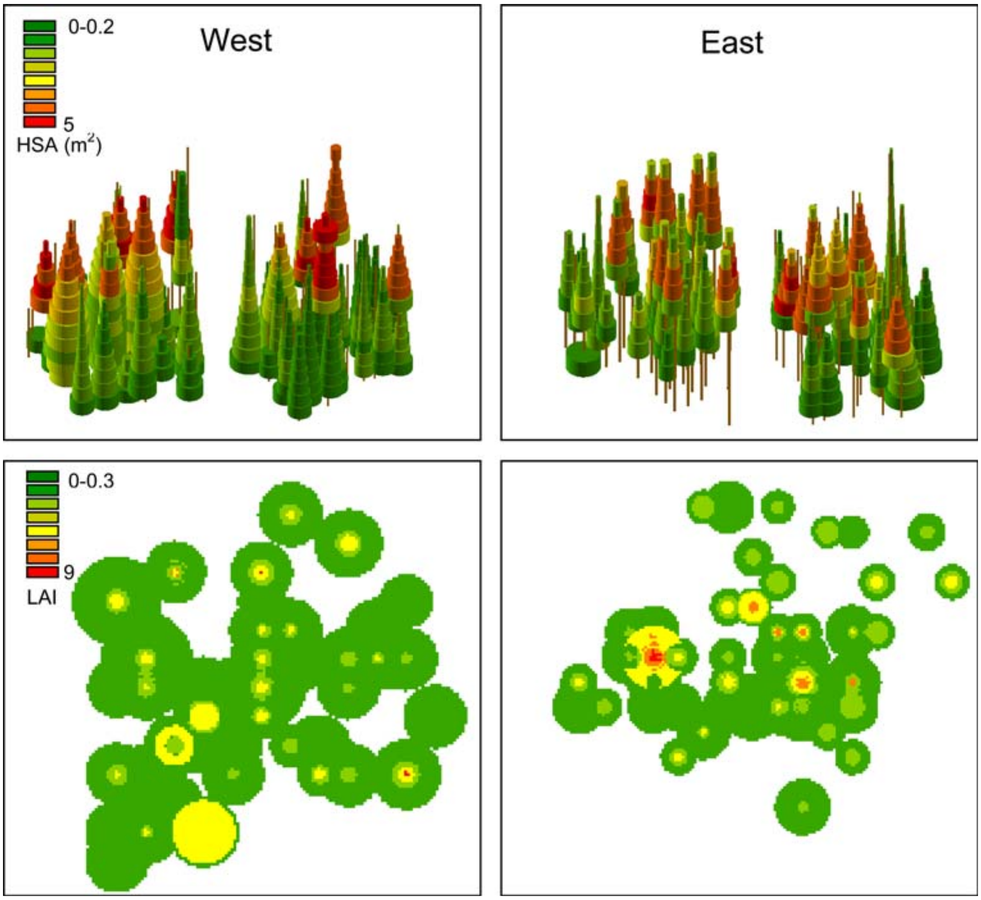

Fig. 5 *Upper panels* Distribution of canopy leaf area in representative plots west and east of the tower. *Each disk* represents a 1-m layer of the crown; the *radius* of each disk is the mean branch length for that layer and the *shading* of the disk corresponds to the hemisurface needle area (*HSA*). *Lower panels* Leaf area index (*LAI*) of representative plots. These plots are presented as examples of what we worked from as we constructed the LAI distribution of the forest

intellectual advantage exists, in that we can use knowledge accumulated from studies at the organismal scale to inform our understanding of processes at the ecosystem scale. In this study, we observed variation in eWUE between two forest communities (Figs. 1, 2, 3). We also identified differences in species abundance between the forest communities, and differences in canopy architecture and needle ecophysiology that were associated with differences in species abundance (Figs. 5, 6, 7). Using these observations, we asked: can we explain the observed differences in eWUE through analysis of lWUE, as the latter is influenced by canopy architecture and species affinity?

The general answer to this question is no. If we look across the entire 9-year record of eddy flux observations, the mean difference in eWUE between the two communities was 19%. Of that 19%, we could attribute 8% to residual differences in atmospheric VPD because westerly winds tend to be slightly drier than easterly winds. This leaves a difference of 11% to be potentially explained by species effects. Taking into account the combined effects of species composition and canopy structure, we could:

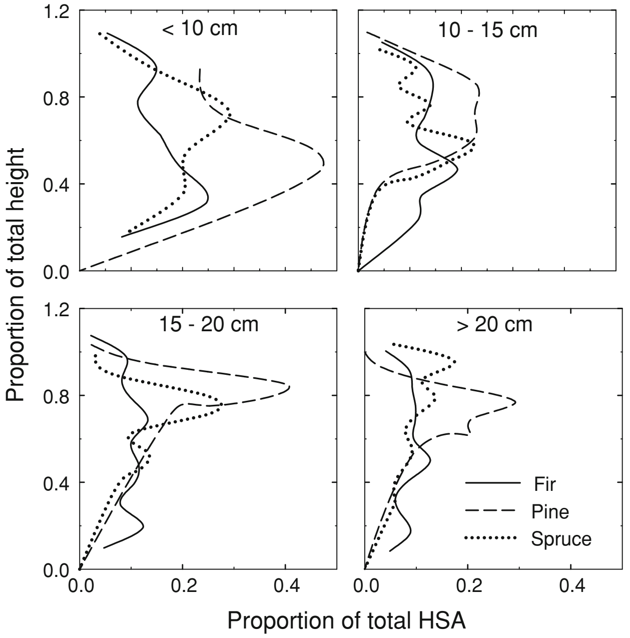

Fig. 6 Proportion of total HSA as a function of the total height of fir (*solid line*), pine (*long dash*) and spruce (*short dash*) trees. Length dimensions (cm) in each panel refer to diameter at breast height, which was used to organize the data into separate classes

(1) explain no significant difference between the two communities using the older needle samples of 2003, which should reflect long-term trends in lWUE (Table 4, physiology plus structure row for >1-year-old needles); (2) explain only 6.3% of the difference in eWUE between the two communities in one of the 3 years examined, using current-year needles, and no significant difference in the other 2 years; and (3) explain only a 3.8–6% difference in eWUE between the two communities using the C isotope ratio of sugars extracted from needles (in this case the difference in eWUE between the two communities and determined from eddy covariance measurements averaged for this one single growing season was 32%; data not shown). Thus, overall, our ability to explain the observed differences in eWUE using species-dependent variation in lWUE, was relatively poor.

In assessing the reasons that needle lWUE failed to explain differences in eWUE we have reached two conclusions. First, observed contrasts in δ^{13}C values, among species and between upper and lower canopy layers, are simply too small to explain more than a small fraction of the differences in eWUE. An examination of the data in Table 2 reveals that differences in needle tissue or needle sugar δ^{13}C values are only 2‰ at most; this translates into a 7% difference in eWUE. Thus, if species were partitioned between the two forest communities in a way that maximized contrasts in δ^{13}C values, the greatest difference we could expect in terms of eWUE is only 7%. Second, there are compensating tradeoffs in eWUE that occur when LAI is partitioned to different species and canopy locations in the two communities. For example, as more leaf area is partitioned to lower parts of the canopy in the spruce-fir community it is also shifted to favor spruce at the expense of pine. In essence, the potentially lower lWUE due to a greater fraction of shade needles is offset by the higher lWUE of spruce. It is possible that the larger difference in eWUE obtained from the eddy covariance data is due to bias in the analysis due to the fact that we only examined flux data when PPFD was relatively high and saturating with respect to NEP. If the photosynthetic WUEs for the dominant species in the two communities were different at lower, non-saturating PPFD, then the “true” difference between the stands (as opposed to the difference detected only with data >700 μmol m^{-2} s^{-1}) would be less than that observed from data collected at the higher PPFD values. In that case, the “true” eWUE values would move closer to the values detected by isotope ratios. However, the isotope data from sun and shade needles make it clear that even at low PPFD, species differences and sun-shade differences in needle WUE remain. Thus, it is more likely

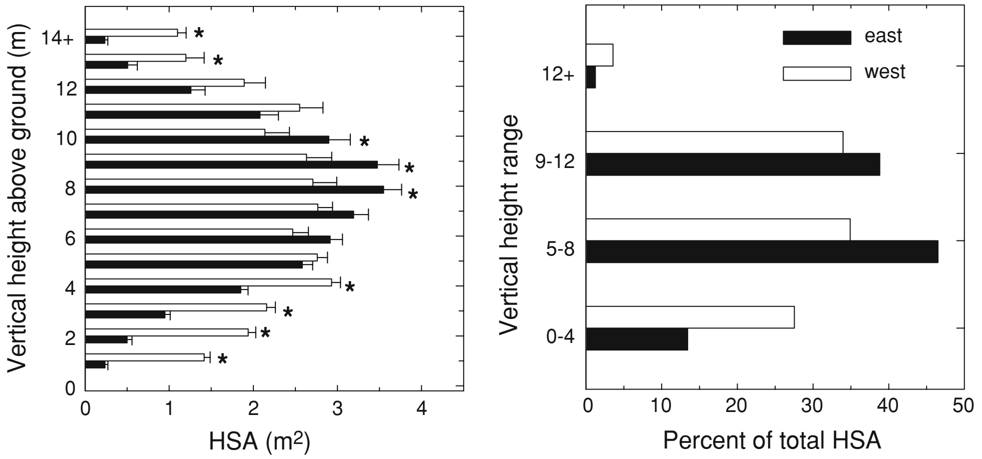

Fig. 7 Total HSA and percent of total HSA in relation to the vertical height above the ground. *Bars* are mean ± SE for trees in plots east (*filled bars*) and west (*open bars*) of the tower location. *$P < 0.05$ (differences between east and west trees)

Table 2 Stable C isotope ratio ($\delta^{13}C$) values (‰) and estimated leaf-scale water-use efficiency (*lWUE*; µmol mmol^{-1}) for bulk tissue of needles older than 1 year, bulk tissue of current-year needles (2003, 2006, 2007), or sugars extracted from needles during different times of the growing season of 2007

Needles >1 year old

	Sun needles						Shade needles					
	Fir		Spruce		Pine		Fir		Spruce		Pine	
	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE
Eastern fetch	−27.46	6.40	−26.11	7.67	−26.97	6.84	−29.24	4.15	−27.71	5.71	−27.86	5.55
	0.13	0.12	0.19	0.17	0.16	0.14	0.11	0.09	0.15	0.11	0.17	0.13
	36	36	36	36	36	36	36	36	36	36	36	36
Western fetch	−27.54	6.33	−26.64	7.17	−26.88	6.19	−29.21	4.52	−27.43	5.92	−27.39	5.92
	0.15	0.13	0.10	0.09	0.12	0.11	0.13	0.06	0.12	0.09	0.14	0.11
	36	36	36	36	36	36	36	36	36	36	36	36

Current-year needles (sun only)

2003						2006						2007					
Fir		Spruce		Pine		Fir		Spruce		Pine		Fir		Spruce		Pine	
$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE
−25.53	8.13	−25.59	8.07	−25.77	7.91	−29.04	4.96	−27.12	6.70	−27.81	6.07	−27.20	5.54	−27.77	6.89	−26.91	6.62
0.20	0.62	0.16	0.15	0.20	0.18	0.29	0.30	0.12	0.13	0.12	0.12	0.27	0.50	0.18	0.46	0.51	0.24
12	12	12	12	12	12	6	6	6	6	6	6	6	6	10	6	6	6

Needle sugars (2007)

	Sun needles						Shade needles					
	Fir		Spruce		Pine		Fir		Spruce		Pine	
	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE	$\delta^{13}C$	lWUE
6 June	−27.68	6.19	−27.59	6.27	−27.02	6.79	−28.38	5.16	−28.64	4.95	−27.76	5.63
	0.53	0.34	0.25	0.16	0.33	0.21	0.38	0.29	0.39	0.30	0.45	0.35
	6	6	6	6	6	6	6	6	6	6	6	6
6 July	−29.04	4.15	−27.33	5.44	−27.07	5.64	−29.39	4.37	−27.77	5.63	−28.16	5.33
	0.24	0.18	0.59	0.44	0.53	0.40	0.39	0.31	0.35	0.27	0.35	0.27
	6	6	6	6	6	6	6	6	6	6	6	6
14 August	−28.10	5.81	−27.84	6.04	−26.76	7.01	−28.52	4.66	−27.07	5.79	−27.43	5.51
	0.66	0.78	0.31	0.28	0.63	0.56	0.66	0.51	0.86	0.66	0.44	0.33
	6	6	6	6	6	6	6	6	6	6	6	6

that eWUE from the eddy covariance observations taken at PPFD <700 µmol m^{-2} s^{-1} will differ between the two stands.

It is likely that soil fluxes (and potentially moss fluxes), and other non-needle fluxes, explain a greater fraction of the difference in eWUE than needle fluxes and associated species effects. We have not been able to conduct a systematic evaluation of ground surface CO_2 and H_2O fluxes in the two communities. We have been able to conduct some measurements of soil respiration rate using chambers at our site including measurements along four 600-m transects running east to west through both forest communities. Respiration was measured during five different 2-week campaigns across 3 years (2002–2003). There were no significant differences in soil respiration rates between the two communities; 4.69 ± 0.15 µmol m^{-2} s^{-1} for the eastern, pine-dominated community and 4.66 ± 0.16 µmol m^{-2} s^{-1} for the western, spruce-fir dominated community. Thus, we cannot at this time attribute differences in eWUE between the two communities to soil respiration rate. There are some differences in the understory communities that may reflect differential H_2O fluxes. For example, the spruce-fir forest exhibits higher ground coverage of both vascular plants and moss, compared to the pine-dominated

Table 3 Results from ANOVA showing effects and interactions between species effects for the three sets of lWUEs obtained from δ^{13}C values as reported in Table 2

	Needles >1 year old (2003)			Current-year needles (sun only)			Needle sugars (2007)		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Species	**2, 422**	**108.24**	**<0.0001**						
Fetch	1, 422	0.04	0.84						
Canopy position	**1, 422**	**502.71**	**<0.0001**						
Species × fetch	2, 422	2.33	0.10						
Species × canopy	**2, 422**	**9.75**	**<0.0001**						
Fetch × canopy	**1, 422**	**7.00**	**0.009**						
Species				**2, 63**	**10.74**	**<0.0001**			
Year				**2, 63**	**65.37**	**<0.0001**			
Species × year				**4, 63**	**4.99**	**0.0015**			
Species							**2, 96**	**8.53**	**0.0004**
Canopy position							**1, 96**	**42.18**	**<0.0001**
Date							2, 96	1.42	0.25
Species × canopy							2, 96	0.70	0.49
Species × date							4, 96	1.52	0.20

Significant terms are shown in *bold*

forest (60 and 17% compared to 29 and 3%, respectively, data not shown). These results could be interpreted to indicate that the spruce-fir dominated forest is characterized by later lasting snow beds with higher mid-summer surface moisture and concomitantly higher beneath-canopy ETs. When combined with slightly drier winds from the west (observed as a higher residual VPD during westerly winds), this could cause higher ET from the spruce-fir community and contribute to lower eWUE. Future studies with more observations and potentially with the use of beneath-canopy flux systems, will be required to fully resolve these possibilities.

We note that one of the underlying assumptions of our analysis is that the δ^{13}C ratio of assimilated C accurately reflects lWUE through Eq. 3 (the linear model). This assumption has been challenged recently in studies that have shown effects on leaf δ^{13}C due to internal (mesophyll) transfer conductance (g_i) and photorespiration (Seibt et al. 2008). The effect of g_i on estimated lWUE occurs because diffusion of CO$_2$ from the intercellular air spaces to the site of carboxylation in the chloroplast causes the fractionation of ^{13}CO$_2$ and ^{12}CO$_2$. This means that some of the signal extracted from differences in δ^{13}C, which is normally attributed entirely to differences in c_i/c_a, and thus lWUE, must be shifted in attribution to include the effect of g_i. In our case, this means that if sun needles have a higher g_i than shade needles, which is entirely possible given past studies (Warren et al. 2003; Terashima et al. 2006), then only part of the difference in δ^{13}C between sun and shade needles can be attributed to differences in c_i/c_a. We attempted to address this concern through a sensitivity analysis. We used both the linear and classic forms of the model relating δ^{13}C to lWUE (sensu Seibt et al. 2008) with the classic form including effects due to g_i and photorespiration. We assumed a rather extreme scenario in which sun needles of all three tree species possess a g_s/g_i ratio 10 times that of shade needles (0.05 for sun needles and 0.5 for shade needles). As expected, the inclusion of g_s/g_i and photorespiration in the model caused a reduction in the estimated lWUE for both sun and shade needles (from $\sim$6.5 to 4.9 and 5.2 to 3.6 μmol mmol^{-1}, respectively). However, when the newly estimated lWUE values were used in the analyses of Table 4 for the needle sugar samples (where the highest difference between the east and west fetches were projected), they caused us to predict a 2.5–3.7% difference in eWUE, rather than a 3.8–6% difference. In other words, inclusion of differential g_s/g_i between sun and shade needles caused us to explain even less of the difference in eWUE between the two communities. Thus, our conclusion that species traits poorly predict eWUE is strengthened not weakened by inclusion of g_i.

Our observations and estimates of eWUE and lWUE are similar in magnitude to those reported in past studies. In a comparative analysis using three ecosystems, grassland, aspen forest and Douglas fir forest, Ponton et al. (2006) focused on periods in the eddy flux record when plant processes, rather than soil processes, were likely to dominate the measure of eWUE. Mean eWUEs were 2.6, 5.4

Table 4 Comparison of lWUE between the eastern and western forest communities using values obtained from the three sets of needles analyzed for δ^{13}C in Table 2 and using Eqs. 5, 6 and 7 (see text)

Effect	Forest fetch[a]	Mean lWUE	% Lower lWUE in western fetch	*F*-value	*P*-value
Needles >1 year old					
Species affinity alone (Eq. 5)	East	6.17 ± 0.04	0	0.874	0.432
	West	6.17 ± 0.04			
LAI distribution alone (Eq. 6)	East (50%)	**6.75 ± 0.04**	**2.7**	**4.62**	**0.030**
	West (50%)	**6.57 ± 0.02**			
Species affinity plus LAI distribution (Eq. 7)	East (25%)	5.78 ± 0.03	0.3	0.60	0.256
	West (25%)	5.76 ± 0.04			
	East (50%)	6.65 ± 0.06	0.6	1.11	0.448
	West (50%)	6.61 ± 0.06			
Current-year needles					
Species affinity plus LAI distribution (2003) (Eq. 7)	East (50%)	7.72 ± 0.04	1.0	2.56	0.110
	West (50%)	7.65 ± 0.02			
Species affinity plus LAI distribution (2006) (Eq. 7)	East (50%)	**6.31 ± 0.09**	**6.3**	**15.62**	**<0.0001**
	West (50%	**5.91 ± 0.06**			
Species affinity plus LAI distribution (2007) (Eq. 7)	East (50%)	6.36 ± 0.06	2.0	3.24	0.09
	West (50%)	6.23 ± 0.04			
Needle sugars (2007)					
Species affinity plus LAI distribution (6 June) (Eq. 7)	East (50%)	**6.55 ± 0.05**	**3.8**	**15.97**	**<0.0001**
	West (50%)	**6.30 ± 0.03**			
Species affinity plus LAI distribution (6 July) (Eq. 7)	East (50%)	**5.48 ± 0.06**	**5.3**	**14.13**	**0.002**
	West (50%)	**5.19 ± 0.05**			
Species affinity plus LAI distribution (15 August) (Eq. 7)	East (50%)	**6.67 ± 0.08**	**6.0**	**18.27**	**<0.0001**
	West (50%)	**6.27 ± 0.05**			

For abbreviations, see Tables 1 and 2

Significant differences are shown in bold

[a] The 50 versus 25% values represent two alternative 607 assumptions about LAI distribution, one in which the sun needles are assumed to only occur in the upper 50% of mean canopy height 608 and one in which they are assumed to occur in the upper 25% of mean canopy height

and 8.1 μmol CO_2 $mmol^{-1}$ H_2O for the three ecosystems, respectively. This type of analysis is similar in concept to what we present in Table 4. On this basis, the eWUE that we estimated for the Niwot Ridge subalpine forest was 5.2–7.7 μmol CO_2 $mmol^{-1}$ H_2O. Law et al. (2002; but modified by personal communication through Ponton et al. 2006) reported eWUE as the slope of gross primary production and ET for an ensemble of coniferous forests to average 4.2 μmol CO_2 $mmol^{-1}$ H_2O, which is slightly higher than the values we observed using the ratio of NEP to ET (Fig. 1). This is to be expected given that our data include ecosystem respiration.

We started this study with a fundamental question as to whether we could bridge the gap between observed differences in needle and ecosystem WUE through explanations based purely on species composition and canopy structure. Our analysis revealed that a significant gap remained, even after accounting for these species effects. Past studies have reported that dynamics in eWUE are likely best explained by photosynthetic processes (e.g., Reichstein et al. 2002; Ponton et al. 2006), although these have been largely restricted to the influence of climate on a single plant community type distributed across time, not the influence of different plant community types on an ecosystem distributed across space. What is unique in our study is that we were able to conduct the analysis using two communities with a similar overall climate and disturbance history. This provided the opportunity to focus on species effects in a more controlled manner than might be available using communities with vastly different functional group assemblages, different climate regimes, and potentially different disturbance histories. Our studies revealed a need to focus more explicitly on non-photosynthetic processes (e.g., soil H_2O fluxes) in order to better resolve differences in eWUE. Complete resolution of the roles played by leaf processes versus soil processes will hopefully lead to deeper insight into how to represent ecosystems in models that describe coupling of the water and C cycles.

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